

A NEW HYBOTINE DIPTERAN FROM THE CRETACEOUS OF BOTSWANA

by S. B. WATERS

ABSTRACT. A Cretaceous dipteran, *Pseudoacarterus orapaensis* gen. et sp. nov. is described from Botswana. It is the only Mesozoic record of the subfamily Hybotinae, and the first fossil assignable to the family Hybotidae from the southern hemisphere. *P. orapaensis* indicates that the Hybotidae originated and diversified at least 40 million years before the previously accepted date. *P. orapaensis* may be ancestral to the extant genera *Sabinios* and *Syndyas*, but not *Acarterus*. The fossil supports predictions of a moist, well-vegetated and seasonal environment in the Cretaceous of this part of southern Africa. Diversification of the Hybotinae appears closely allied with that of the angiosperms.

OF the variety of insect orders represented in the Orapa collection, the dipterans are among the most abundant (Waters, 1989). Many of the insects are superbly and unusually well preserved; many whole-bodied organisms have been found, some having retained an exquisite amount of detail. Described here is the first Mesozoic record of the subfamily Hybotinae, and the first fossil hybotid fly from the southern hemisphere.

GEOLOGICAL SETTING

The fossil site, located over a large diamondiferous kimberlite pipe (number 2125A/K1) in north-central Botswana, is just over 220 km due west of Francistown (21° 17' S, 25° 21' E, approximately 960 m above sea level). The eruption of the kimberlite produced a large volcanic crater which later filled with sediments. Mining operations have revealed that there are at least 200 m of sediments comprising decomposed kimberlitic material. Five facies are recognised: 1, volcanogenic and talus slope deposits; 2, fluvial deposits; 3, debris flow deposits; 4, granular mass flows; and 5, fine grained sediments.

Sediments in the form of screes and talus (1–4), which were deposited as coarse mudflows, have, to date, yielded few fossils. However, the fine grained shales and mudstones (5), which were deposited within a small crater lake, have been a rich source of superbly and unusually well-preserved material. This includes whole-bodied organisms (an arachnid and many insects) as well as plant fragments. Among the insects are Coleoptera, Blattoidea, Diptera, Hymenoptera, Hemiptera, Orthoptera, Neuroptera and Dermaptera. The Diptera are among the most abundant in the collection (Waters 1989). Specimens are preserved as coalified compressions (*sensu* Schopf 1975) on the bedding surfaces of the laminated shales and mudstones.

Several kimberlite pipes (including Orapa) within the Transvaal Craton, have given radiometric ages ranging between 95.4 and 87.7 Ma (Davis 1977). Orapa has been so dated at 93.1 Ma or late Cretaceous in age. The dates are based on estimates of the accumulation of lead isotopes (the decay products of uranium) within zircon crystals in the kimberlite. Additional results from fission track dating of the Orapa zircons have given results of 84.4 ± 5.7 Ma, and 92.4 ± 6.1 Ma (Haggerty *et al.* 1983). A palynological study carried out on the sediments also indicates an early Upper Cretaceous age (Scholtz pers. comm.).

These radiometric dates represent the time of eruption of the kimberlite, or, more correctly, the time of the lowering of the temperature of the zircons below 1200 °C (McKay and Rayner 1986). However, it seems likely from the nature of the erupted kimberlite, the sediments, and the basin,

that the crater would have taken little time to fill, perhaps less than 0.5 Ma (McKay and Rayner 1986). Therefore, the age difference between the kimberlite and the sediments may be slight.

METHODS AND MATERIAL

The fossil was examined using a Zeiss SV8 microscope. It was photographed using polarized light, with a Zeiss Pyramid photomicroscope. The specimen was drawn by projecting the photograph on to tracing paper with an enlarging camera and with the aid of a camera lucida.

Morphological terminology is based on McAlpine (1981) and the arrangement of species into higher taxa follows that of Chvala (1983).

SYSTEMATIC PALAEOLOGY

Superfamily EMPIDOIDEA (*sensu* Chvala 1983)

Family HYBOTIDAE Chvala, 1983

Subfamily HYBOTINAE (*sensu* Chvala 1983)

Genus PSEUDOACARTERUS gen. nov.

Type and only known species. Pseudoacarterus orapaensis sp. nov.

Derivation of generic name. Greek: *pseudēs*, false, and *Acarterus*, the extant genus most closely resembling the fossil.

Diagnosis. Legs slender with well-developed chaetotaxy, one pair, presumably the hind pair, with thickened femora; haltere with long, elongated stalk and large pear-shaped knob, both with well-developed chaetotaxy; characteristic Hybotidae and Hybotinae wing morphology and venation; wing length > 2.47 mm, breadth 0.99 mm, clear, with stigma from just in front of R1 to R2 + 3; blade uniformly covered in microtrichia, costal vein with stouter hairs, other veins bare; well-developed axillary lobe; C ends at tip of M1; Sc is closely associated with R1 distally and joins it far beyond radial bifurcation; all longitudinal veins simple; R4 + 5 and M1 parallel, radial sector a little shorter than length of basal cells br and bm; br and bm long, a third of wing length, vein separating them weakly developed; A1 reduced; dm large, elongated, lies near distal end of wing and has two veins issuing from it, both veins simple and complete; cup present, equal in length to br and bm.

Pseudoacarterus orapaensis sp. nov.

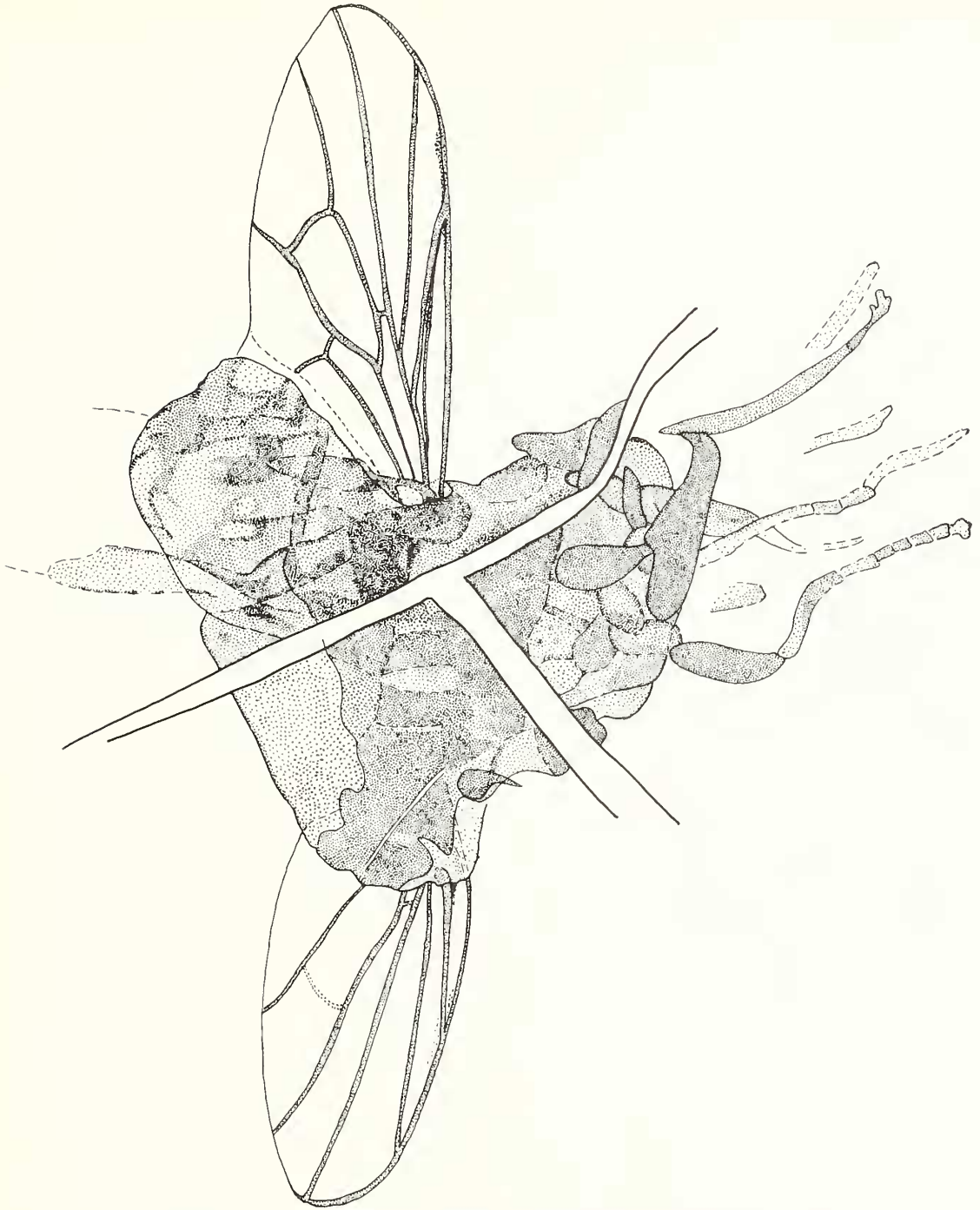
Plate 77; text-figs. 1–3

Holotype. Bernard Price Institute for Palaeontological Research, University of the Witwatersrand; Johannesburg, South Africa; available as part, No. BP/2/25224a (Pl. 77, figs. 1–3; text-fig. 1) and counterpart, No. BP/2/25224b (Pl. 77, figs. 1–3; text-fig. 2), from the Upper Cretaceous grey mudstones of Orapa, Botswana.

Derivation of name. Site of discovery: Orapa.

Diagnosis. As for the genus.

Description. The abdomen, head and thorax of *Pseudoacarterus* are crushed, and obscure a third of the right wing and a quarter of the left wing; most of the venation is visible in the left wing of the part (Pl. 77, fig. 1; text-figs. 1 and 3). Bristles have been observed on some areas of the body (Pl. 77, fig. 2). Whether these are on the thorax and/or on the abdomen is uncertain, as individual segments are not easily distinguishable. These non-differentiated hairs may be as long as the knob of the haltere. The haltere is found just above the right wing of the part (Pl. 77, figs. 1 and 2; text-fig. 1) and is 0.41 mm long. The body is approximately 2.50 mm long (although this measurement is misleading because the dipteran lies over another insect (a non-dipteran, as a small hind-wing is detectable) and the bodies of these two insects are not easily distinguishable from one another). The wing span is 5.42 mm. The most complete wing of the hybotid (the left wing of the part) measures 2.47 mm long and 0.99 mm broad at the widest point.



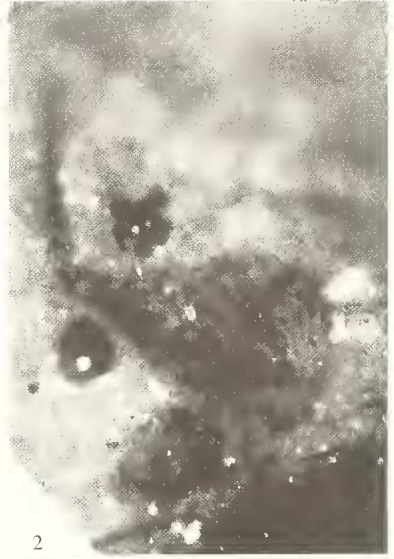
TEXT-FIG. 1. *Pseudoacarterus orapaensis*, BP/2/25224a, whole specimen, $\times 32.1$.

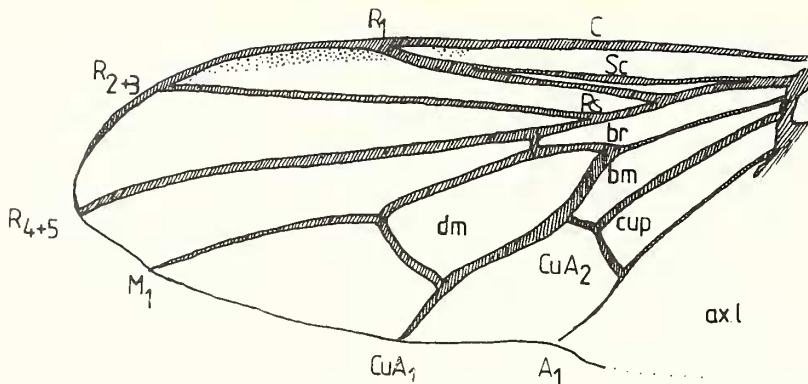


TEXT-FIG. 2. *Pseudoacarterus orapaensis*, BP/2/25224b, whole specimen, $\times 27.5$.

EXPLANATION OF PLATE 77

Pseudoacarterus orapaensis, gen. et sp. nov., Upper Cretaceous, Orapa, Botswana. Figs 1–3, BP/2/25224a. Fig. 4, BP/2/25224b. 1, whole specimen, $\times 16.8$. 2, Haltere, $\times 102.4$. 3, Tibia and tarsi with two pectinate claws, $\times 209$. 4, Whole specimen, $\times 21.8$.





TEXT-FIG. 3. *Pseudocarterus orapaensis*, BP/2/25224a and b. Composite drawing of the wings (left and right of part and counterpart). $\times 40.5$. A1, branch of anal vein; C, costa; CuA1 and CuA2, anterior branches of cubitus; M1, posterior (sectoral) branch of media; R1, anterior branch of radius; R2+3 and R4+5, posterior (sectoral) branches of radius; Rs, radial sector; Sc, subcosta; ax.l, axillary lobe; bm, basal medial cell; br, basal radial cell; cup, posterior cubital cell; dm, discal medial cell.

Fragments of five legs are preserved. The legs are elongated, the longest, presumably the hind leg, is 2.36 mm long and has a thickened femur. Femora, tibia and tarsi are bristled. The complete femur of the counterpart (Pl. 77, fig. 4; text-fig. 2) bears long, fine hairs (longer than width of segment) on the one side, presumably the ventral side, only. The tibia and tarsi however, which are all long and equally slender (Pl. 77, fig. 3), are uniformly covered with much shorter hairs (a third of the width of the segments). At the end of the last tarsal segment two pectinate claws are present (Pl. 77, fig. 3); no further details of the pretarsus are distinguishable. No tibial gland is visible.

The haltere (Pl. 77, fig. 2) consists of a narrow elongate stalk with a large pear-shaped knob; the narrow end of the 'pear' is attached to the stalk. The knob is eight times as wide as the stalk. Both sections of the haltere are covered with especially fine short hairs, each about as long as the width of the stalk.

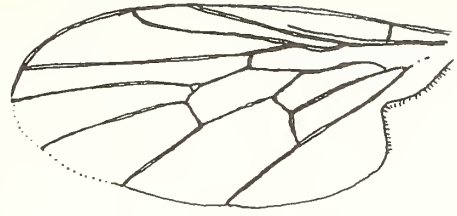
The wings are large and narrowly elliptical (Pl. 77, figs. 1 and 4; text-figs. 1-3). The membrane is entirely and uniformly covered with microtrichia. The costal vein bears slightly longer and stouter hairs. All other veins are bare. By combining the drawings of both the left and right wings of the part and counterpart, a composite drawing has been made which illustrates venational details (text-fig. 3). The wings are clear with a somewhat darker, narrow, and elongate stigma. The stigma extends from just prior to the R1 vein to the R2+3 vein. The axillary lobe is presumably well developed (the blade, at a quarter of the distance from the wing's point of origin, is approximately as wide as the rest of the blade; the wing-margin has thus not turned towards the anterior of the wing yet, suggesting a large lobe). The costal vein (C) ends at the tip of the 4th longitudinal vein M1. The auxiliary vein (Sc) is closely associated with R1 distally; Sc joins R1 far beyond the radial bifurcation. The longitudinal veins: R2+3, R4+5, and M1 are simple. R4+5 and M1 are parallel. The radial sector is long, not much shorter than the basal section of M which separates the basal cells br and bm. The discal vein M between the basal cells br and bm is indistinct. The discal cell (dm) is large and elongated and lies relatively near the wing's edge. It has two veins issuing from its distal end and it is approximately as long as the anterior vein. Both veins M1 and CuA1 join the wing-margin. The anal cell (cup) is present and is about as long as the basal cells; the vein closing it, CuA2, reaches the anal vein at right angles. The basal cells br, bm, and cup are long, being greater than a third of the length of the wing. The 6th longitudinal vein A1 is weakly developed, it is not certain whether it reaches the hind-margin of the wing.

DISCUSSION

Biology

The family Hybotidae includes about 1300 extant species (Chvala 1983). They are small to medium sized flies measuring 1.5-12 mm (Steyskal and Knutson 1981). They are recognized mainly by the brachycerous-type wing venation and their general predatory appearance (Colless and McAlpine

TEXT-FIG. 4. Wing of *Trichinites cretaceus*, after Hennig (1970).



1970). One of the three pairs of legs are raptorial; these have thickened femora probably accommodating strong muscles (Smith 1969). The proboscis is adapted for piercing. The eyes are large, often with enlarged upper ommatidia.

Adults are predominantly predacious on smaller arthropods (Colless and McAlpine 1970), usually on other Diptera (Barraclough and Londt 1985); Kessell (1955) and Downes (1970) also mention cannibalistic tendencies. Prey may be live or dead (Downes and Smith 1969). In the Hybotidae (Poulton 1907, 1913), the predacious habit is usually exhibited by both sexes. Members of this family (and related families) however, are not exclusively predacious as both sexes may visit flowers to feed on nectar (Laurence 1955; Downes and Smith 1969; Downes 1970; Steyskal and Knutson 1981). Adults are mostly found among undergrowth and in shady woods, bush, grassland and moist vegetation near water. They have also been observed on tree trunks and on the surface of water.

The immature stages are little known, but they appear to be predacious (Smith 1969). Larvae of most Hybotinae (Tuomikoski 1966) live in terrestrial habitats such as soil, leaf-litter, rotting wood or dung; a few species live in intermediate situations (e.g. surfaces covered by a thin film of water) and some are aquatic.

At least two-thirds of the species of the subfamily Hybotinae are found in the tropics and subtropics of the Oriental and Neotropical regions (Chvala 1983). Three common southern African genera allied to *P. orapaensis* are *Sabinios*, *Syndyas*, and *Acarterus*. The former two extant genera are found mainly in the Cape coastal region, and *Acarterus* (with its single species, *A. unicolor*) is an entirely Afrotropical genus (Smith pers. comm.). Specimens of all three genera have been reported from the southern coastal regions in general, and as far north as Zimbabwe. These regions are moist and often well wooded. The absence of members of the subfamily in the drier open regions, including the Limpopo coastal region, is obvious (Smith 1969).

The morphology of the fossil is so similar to that of living dipterans, that I suggest their environmental requirements were the same. Environmental stability over time ensures few or no changes in the physiology and morphology of an organism to be necessary (Coope 1977). I therefore suggest that humid conditions (and seasonal rainfall?) and forested or well-vegetated surroundings prevailed at Orapa during this part of the Cretaceous. Part of the explanation may lie in the position of Africa at the time of deposition of the sediments – the continent was approximately 15° to the south of its present position; Orapa was about where Cape Town is today. This may have produced a similar environment.

Morphology

Wings. The family Hybotidae, comprising the three subfamilies Tachydromiinae, Hybotinae and Ocydromiinae, is characterized by several autapomorphies. Of these, the only ones recognizable in the Orapa specimen are related to wing venation (i.e. the radial sector has only two branches, and the vein R4+5 is not forked).

Characteristics typical of extant members of the subfamily Hybotinae are listed below; most are shared with the Cretaceous specimen but I indicate where this does not occur.

1. Wings often have an apparent costal stigma.
2. Wings have a more or less developed axillary lobe and no alula (the latter is not distinguishable in *P. orapaensis*).

3. The discal cell is present, emitting 2 veins (M2 absent) to the wing margin.
4. The anal cell (cup) is large, at least as long as or longer than basal cells (in *Pseudoacarterus* the anal cell is as long as the basal cells).
5. Radial sector rather short, somewhat longer in *Syneches*, *Stenoproctus*, *Acarterus*, *Afrohybos* and *Parahybos* (in *Pseudoacarterus* the radial sector is of intermediate length).

The only two plesiomorphic features of the wing of the *Orapa* specimen are the long basal cells and the large anal cell. All other characters are apomorphic. The wings of *P. orapaensis* resemble those of the extant genera *Sabinios*, *Syndyas* and *Acarterus* but are most similar to those of *Acarterus*.

Legs. The hind femora of members of the Hybotinae are usually more or less swollen and bristled as is the case in the genera *Sabinios*, *Syndyas* and the fossil *Pseudoacarterus*. This is not so in *Acarterus*.

Another distinguishing feature of the family Hybotidae is the gland on the fore-tibia. This is not observable in the fossil because only a few segments of the six legs are preserved, the front segments not being among these. Overall, the hybotid displays a greater number of apomorphic than plesiomorphic morphological characteristics.

Classification

The phylogeny of the Diptera has been studied and discussed by many authors (e.g. Rohdendorf 1974; Hennig 1981). The phylogeny of the superfamily Empidoidea has been best researched by Hennig (1981) and Chvala (1981, 1983). Morphologically, *Pseudoacarterus orapaensis* undoubtedly belongs to this group.

The placement of this new genus *Pseudoacarterus* in higher taxa follows the recent system of Chvala (1983), who studied all available type material, including 14000 specimens from many parts of the world, but mainly Europe, and in particular Scandinavia. Workers have supported this arrangement indirectly (Colless 1963; Tuomikoski 1966; Hennig 1970, 1971; Chvala 1981). Chvala (1983, p. 9) regarded the family Empididae as 'an unnatural paraphyletic unit' and, depending on the authority, it comprised about eleven subfamilies. Chvala suggested splitting the former Empididae into four distinct families: Empididae, Hybotidae, Atelestidae, and Microphoridae. These, together with the Dolichopodidae comprise the superfamily Empidoidea (text-fig. 5).

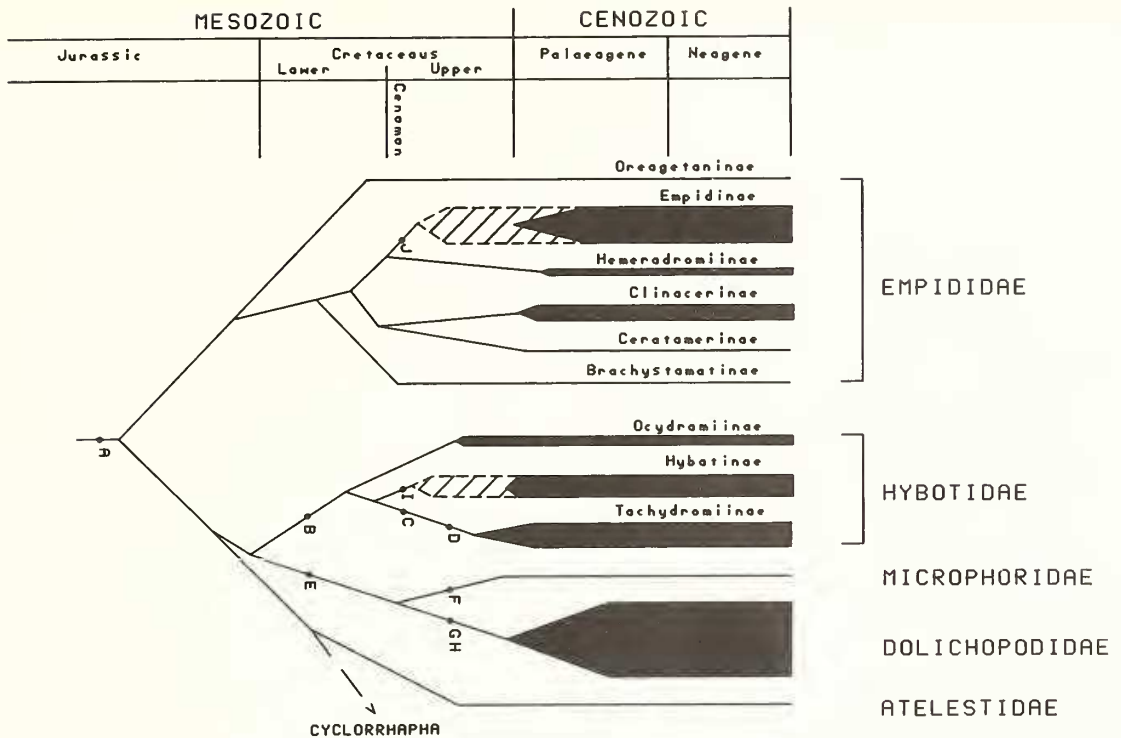
Phylogeny. Chvala (1981, 1983) discussed the phylogenetic patterns of the Empidoidea. I have taken his phylogeny and added two *Orapa* fossils: *Pseudoacarterus*, and an empid, *Empis orapaensis* (Waters, 1989) (text-fig. 5).

The wings of *Pseudoacarterus*, being the only parts available for close study, do not provide sufficient information for changes to be made to the arrangement of groups as shown in text-fig. 5. Other morphological details are required (e.g. chaetotaxy of thorax and structure of genitalia). However, the date of the origin of the Hybotidae is considerably earlier than the 70 Ma supported by Chvala (1983).

Diversification of the Hybotidae coincided with the rise to dominance of the flowering plants. The nectar-feeding habit of these flies may indicate a close evolutionary relationship.

Of the three subfamilies of the Hybotidae: Ocydromiinae, Hybotinae, and Tachydromiinae, the latter two are more closely related, on the basis of the loss of M2 (Hennig 1970). Hennig (1970) considered the Ocydromiinae to be a sister group of the Tachydromiinae and Hybotinae.

Trichinites cretaceus (wing illustrated in text-fig. 4) was considered by Hennig (1970) and Chvala (1983) to be the forerunner of these three subfamilies since it displays several of the groundplan characteristics (e.g. large anal cell, cup). The large anal cell is also assumed to be a part of the groundplan of the Hybotinae. The presence of an even larger anal cell in some genera (e.g. *Hybos*), and a short anal cell (as in the Ocydromiinae) are derived features (Hennig 1970). The anal cell of the *Orapa* fossil is proportionally the same size as that of *Trichinites cretaceus* (it is as long as the two basal cells), and this primitive feature therefore suggests *Pseudoacarterus* to be a forerunner of a number of hybotid groups.



TEXT-FIG. 5 Presumed phylogeny of the Empidoidea. A–J, fossil finds in support of phylogenetic scheme. A–H, after Chvala (1983); I–J, fossils from Orapa, Botswana. Shaded areas represent relative numbers of extant species; hatched areas represent the earlier origins predicted for the two Empidoidea families from Orapa. A, *Protempis* (Protempididae); B, *Trichinites*; C, *Cretoplatypalpus*; D, *Archiplatypalpus*; E, *Microphorites*; F, *Cretomicrophorus*; G, *Archichrysotus*; H, *Retinitus*; I, *Pseudoacarterus orapaensis*; J, *Empis orapaensis* Waters.

Trichinites also displays the plesiomorphic characteristics of having three M veins emitting from the discal cell and having all the venational elements (cells and the points of origin of various veins) nearer the wing base. The veins are thus longer than those of some more recent species. *Pseudoacarterus orapaensis*, however, exhibits apomorphic character states; it has only two M veins (having lost M2) and it has the venational elements nearer the wing tip. Veins (for example, M1 and M3) are thus shortened.

Pseudoacarterus excludes the Ocydromiinae as a possible descendant as its members have either a very short anal cell, for example the genus *Ocydromia*, or they have three M veins issuing from the discal cell, for example the genus *Stuckenbergia*. The subfamily Tachydromiinae is also excluded as it does not have a discal cell.

Members of the subfamily Hybotinae are, therefore, the only descendants of *Pseudoacarterus*. Extant genera which resemble this fossil are, as previously mentioned, *Sabinios*, *Syndyas*, and *Acarterus*. As nearly all species of the Hybotinae have swollen and bristled hind femora, a comparatively large anal cell and a distinct vein M between the two basal cells br and bm, I suggest that these characteristics are part of the groundplan of the subfamily. *Pseudoacarterus* does not display all these features and I therefore do not consider it an ancestor of all Hybotinae genera. The faint M vein between its two basal cells suggests it could be ancestral to *Sabinios* and *Syndyas* as both display this feature; I do not believe that this derived feature arose independently in more than one group. However, these two genera have other derived characters which they do not share with *Pseudoacarterus* such as the shortening of Rs (by the displacement of its point of origin towards the

wing tip). *Sabinios* and *Syndyas* have a considerably larger number of apomorphic wing venational characters. In *Acarterus*, on the other hand, the portion of vein M between the two basal cells is distinct. I suggest that *Acarterus* branched away from the main line as a separate genus before the appearance of *Pseudoacarterus*, thereby possibly sharing another more ancient and as yet unknown ancestor. This difference in the venation of the extant and the extinct genus is, however, the only one, and explains the name of this newly found specimen.

Trichinites has no distinct swelling or bristling of any of the legs, or a portion of them, and it is not certain whether this was a part of the groundplan of the Hybotidae or of the Empidoidea in general. Swelling of femora or tibiae of the raptorial legs occurs in several groups within the superfamily. For example, the Hemerodromiinae of the family Empididae display this condition as do the Hybotinae and Tachydromiinae of the Hybotidae. It seems likely that this condition arose independently a number of times. The extant genus *Acarterus* does not exhibit swelling or bristling, in contrast to *Pseudoacarterus*, *Sabinios* and *Syndyas*. This supports my suggestion that *Pseudoacarterus* is more closely related to *Sabinios* and *Syndyas* than it is to *Acarterus*, and may indeed be the common ancestor of *Sabinios* and *Syndyas*.

Acknowledgements. I thank the Office of the President and the National Museum of Botswana, and the De Beers Botswana Mining Company for allowing the collection of fossils. I should like to thank the CSIR and the University of the Witwatersrand for financial support, and Dr C. Feather of AARL for permission to use his company's microscope. My thanks are also due to Drs K. G. V. Smith and R. J. Rayner for comments on early drafts of the manuscript, and K. R. K. Waters for advice and encouragement. This is an OHSG publication.

REFERENCES

- BARRACLOUGH, D. A. and LONDT, J. G. H. 1985. Diptera. In SCHOLZ, C. H. and HOLM, E. (eds.). *Insects of Southern Africa*, 283–326, Butterworth, Durban.
- CHVALA, M. 1981. Classification and phylogeny of Empididae, with a presumed origin of Dolichopodidae (Diptera). *Ent. scand. Suppl.* **15**, 225–236.
- 1983. The Empidoidea (Diptera) of Fennoscandia and Denmark. II. General part. The Families Hybotidae, Atelestidae and Microphoridae. *Faun. Ent. Scand.* **12**, 9–257.
- COLLESS, D. H. 1963. An Australian species of *Microphorella* (Diptera: Empididae), with notes on the phylogenetic significance of the genus. *Proc. Linn. Soc. N.S.W.* **88**, 320–323.
- and McALPINE, D. K. 1970. Diptera. In CSIRO, *Insects of Australia*, xiii + 1029 pp. Melbourne University Press, Melbourne.
- COOPE, G. R. 1977. Fossil Coleopteran assemblages as sensitive indicators of climatic changes during Devensian (Last) cold stage. *Phil. Trans. R. Soc. Lond.* **B280**, 313–340.
- DAVIS, G. L. 1977. The ages and Uranium contents from Kimberlites and associated rocks. *Extended abstracts: 2nd international Kimberlite conference*, Santa Fé.
- DOWNES, J. A. 1970. The feeding and mating behaviour of the specialised Empidinae (Diptera); observations on four species of *Rhamphomyia* in the high arctic and a general discussion. *Can. Ent.* **102**, 769–791.
- and SMITH, S. M. 1969. New or little-known feeding habits in Empididae (Diptera). *Can. Ent.* **101**, 404–408.
- HAGGERTY, S. E., RABER, E. and NAESER, C. W. 1983. *Earth plan. Sci. Letts.* **63**, 41–50.
- HENNIG, W. 1970. Insektenfossilien aus der unteren Kreide. II. Empididae (Diptera, Brachycera). *Stutt. Beitr. Nat.* **214**, 1–12.
- 1971. Insektenfossilien aus der unteren Kreide. III. Empidiformia ('Microphorinae') aus der unteren Kreide und aus dem Baltischen Bernstein; ein Vertreter der Cyclorrhapha aus der unteren Kreide. *Stutt. Beitr. Nat.* **232**, 1–28.
- 1981. *Insect phylogeny*, 514 pp. Wiley, New York.
- KESSEL, E. L. 1955. The mating activities of balloon flies. *Syst. Zool.* **4**, 97–104.
- LAURENCE, B. R. 1955. The Empididae (Diptera) of a Yorkshire stream. *Ent. mon. Mag.* **91**, 220–224.
- McALPINE, J. F. 1981. 2. Morphology and terminology – adults. In McALPINE, J. F. et al. (eds.). *Manual of Nearctic Diptera.*, Vol. 1. Agriculture Canada, Ottawa: Monograph 27, 9–63.
- McKAY, I. J. 1987. *Fossil Carabids from Orapa, Botswana*. M.Sc. thesis (unpubl.). University of the Witwatersrand, Johannesburg, South Africa.

- and RAYNER, R. J. 1986. Cretaceous fossil insects from Orapa, Botswana, *J. ent. Soc. S.A.* **49**, 7–17.
- POULTON, E. B. 1907. Predaceous insects and their prey. *Trans. ent. Soc. Lond.* **1096**, 323–409.
- 1913. Empididae and their prey in relation to courtship. *Entomol. mon. Mag.* **49**, 177–180.
- RAYNER, R. J. 1987. March flies from an African Cretaceous springtime. *Lethaia*, **20**, 123–127.
- and MCKAY, I. J. 1986. The treasure chest of the Orapa diamond mine. *Botswana Notes Recs.* **18**, 55–61.
- ROHDENDORF, B. 1974. *The historical development of Diptera*, 360 pp. University of Alberta Press, Alberta.
- SCHOPF, J. M. 1975. Modes of fossil preservation. *Rev. Palaeobot. Palynol.* **20**, 27–53.
- SMITH, K. G. V. 1969. The Empididae of Southern Africa. *Ann. Natal Mus.* **19**, 1–347.
- STEYSKAL, G. C. and KNUTSON, L. V. 1981. 47. Empididae. In McALPINE, J. F. *et al.* (eds.). *Manual of Nearctic Diptera*, Vol. 1. Agriculture Canada, Ottawa: monograph 27, 607–625.
- TUOMIKOSKI, R. 1966. The Ocydromiinae group of subfamilies (Diptera, Empididae). *Ann. Ent. Fenn.* **32**, 282–294.
- WATERS, S. B. 1989. A Cretaceous dance fly (Diptera: Empididae) from Botswana. *Syst. Ent.* **14**, 233–241.

S. WATERS

Bernard Price Institute for
Palaeontological Research
University of the Witwatersrand
WITS 2050
South Africa

Typescript received 28 June 1988

Revised typescript received 15 August 1988